

The zoogeographic implications of the prosobranch gastropods of the Moín Formation of Costa Rica

David G. Robinson

Malacology/Invertebrate Paleontology, Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

Abstract: The deposits of the Moín Formation are located in and around the town of Puerto Limón, on the Caribbean coast of Costa Rica. The fossils date the formation as being Late Pliocene to early Pleistocene in age. The systematics of its constituent prosobranch gastropods were studied, and comparisons made with Recent and fossil gastropod faunas in the Caribbean area. Seventy-one percent of the taxa are living species and for most, this is their first occurrence in the fossil record. These are primarily Caribbean species, but West African/Mediterranean, Panamic and Indo-Pacific elements are also present. Twenty-one percent of the taxa are endemic to these beds, and 8% are typically Mio-Pliocene species occurring for the last time in the fossil record.

A number of species characteristic of the Moín formation have a Holocene distribution in the western Caribbean, extending approximately from the Gulf of Honduras to the northern coast of Colombia, while others have a southern Caribbean distribution, from Costa Rica to across northern South America. These zoogeographic patterns are not well-defined, however, and based on the prosobranch species occurring in the Moín Formation, the existence of specific faunules or other zoogeographic entities in the southwestern Caribbean area cannot be supported.

The deposits of the Moín Formation crop out primarily west and northwest of the town of Puerto Limón on the Caribbean coast of Costa Rica. Historically, the formation has been considered to consist of some 70 m of dark blue claystone to loosely consolidated blue sandy clay with indistinct bedding due to extensive bioturbation, with interbedded lenses of coral reef material. Where bedding is visible, it dips at an angle of 1-2° to the north (Cassell, 1986). With the exposure by bulldozing associated with the urbanization of the peninsula, these beds weather to a reddish-orange clay, with well-preserved fossils eroding out so that they can be easily collected.

Workers in the past have dated the Moín Formation as Miocene or Pliocene in age (Gabb, 1881; Olsson, 1922; Woodring, 1928) using traditional dating methods such as percentages of living species involving Lyellian curves. More recently, using micropaleontological evidence, the Moín Formation has been considered to be early Pleistocene in age (Akers, 1972; Taylor, 1975; Robinson, 1990, 1991) and it has been suggested that the topmost beds extend into the middle Pleistocene (Akers, pers. comm.) or even late Pleistocene (Cassell, 1986). However, Coates *et al.* (1992), have expanded the definition of the Moín Formation, adding another 130 m of underlying sediments, placing most of the formation in the Late Pliocene, with only the topmost strata falling in the Pleistocene. This expanded definition shall remain open to question for the present.

METHODS

Extensive collections of fossil material from the area were made over several years, and the collections made by earlier Tulane University researchers, primarily Drs. Harold and Emily Vokes, were incorporated. The full geographic extent of the Moín Formation is not clearly established, but is believed to underlie most of the tropical forest on the higher elevations of the Limón Peninsula. The collection of fossil material has tended to be opportunistic in nature, being possible only in "windows" of short duration, occurring when briefly exposed by bulldozing of the vegetation preparatory to urban expansion of Puerto Limón. If not immediately built upon, the land is rapidly reclaimed by secondary forest growth within a few months. The molluscs collected from the Moín Formation were compared with taxa from other Caribbean faunas, in particular Mio-Pliocene Gurabo and Cercado Formations of the Dominican Republic, the Pinecrest and Caloosahatchee Formations of Florida, the Agueguexquite Formation of the Isthmus of Tehuantepec, the Limón and Gatún Formations of the Panamic Isthmus, the Cantaure Formation of Venezuela, and the Esmeraldas beds of Ecuador. Of particular importance for comparison were the faunas of the Bowden Formation of Jamaica, the Cabo Blanco Group of Venezuela and the Bermont of Florida, as they are closer in age to the Moín and provide a chronological context for the study. The systematics of all constituent species had to be

examined with care because of the perspective adopted by the first molluscan systematists working with these various formations. In many cases, the assumption was made that these beds were by and large contemporaneous, and the molluscan taxa contained in one particular formation were therefore common to others. With the increasing accuracy of dating using foraminifera and calcareous nannoplankton indicators, these circum-Caribbean beds are now known to range in age from Miocene to Pleistocene. Many of the molluscan species can now be seen as distinct, as opposed to being regional variants of more widespread taxa, particularly when they can be studied together in a more clearly-defined geographical and chronological context. During this study, collections of comparative Recent shallow-water material were also made from the western Caribbean region, from the Yucatán Peninsula, and the Caribbean coasts of Honduras, Costa Rica (Robinson and Montoya, 1988), and Panamá and Colombia. Deeper water material was collected from the Honduran continental shelf from on board Honduran shrimp boats. Ecological data from living specimens were used to interpret the paleoecological conditions under which the Moín Formation was deposited.

RESULTS

Three hundred and six prosobranch gastropods were identified in this study, and the systematics as well as the paleoecology of these species are currently in preparation. It should be understood that this paper is a preliminary report, with further analysis of the systematics and phylogenetic relationships of the species currently in progress, but some conclusions of interest can already be made.

Effects of the Plio-Pleistocene glaciations

A substantial proportion of the rich Moín fauna (65 species), approximately 21% of the total, appears to be restricted to these beds. The deposition of the portion of the Moín Formation focused on in this study is interpreted here as occurring during a warm interglacial period, which resulted in a short-lived speciation event. While some of these species have already been described (Table 1), a large proportion have not. More collecting needs to be done in the southwestern Caribbean to confirm that all of these species are indeed extinct.

Another 8% of the Moín taxa (24 species) represent the last occurrence in the fossil record of a number Mio-Pliocene taxa typical of older fossil beds, including the Bowden, Pinecrest, Cantaure, Gatún and Río Banano Formations (Table 2). Of interest are a number of species that are illustrative of the effects of the initial Plio-Pleistocene glacial pulses. By the time the Moín Formation

Table 1. Previously described taxa endemic to the Moín Formation.

<i>Calliostoma limonensis</i> Olsson, 1922	<i>Latirus irazu</i> Olsson, 1922
<i>Calliostoma castilla</i> Olsson, 1922	<i>Agaronia mancinella</i> (Olsson, 1922)
<i>Turbo pittieri</i> Dall, 1912	<i>Olivella limonensis</i> Olsson, 1922
<i>Cochliolepis simplex</i> (Gabb, 1881)	<i>Mitra poas</i> Olsson, 1922
<i>Atlanta ammonitiformis</i> Gabb, 1881	<i>Nebularia coralliophila</i> Olsson, 1922
<i>Cerithiopsis limonensis</i> (Gabb, 1881)	<i>Prunum limonensis</i> (Dall, 1896)
<i>Aclis microsculpta</i> Gabb, 1881	<i>Conus trisculptus</i> Pilsbry and Johnson, 1917
<i>Chicoreus prolixus</i> E. Vokes, 1974	<i>Conus ultimus</i> Pilsbry and Johnson, 1917
<i>Calotrophon ascensus</i> E. Vokes, 1976	<i>Conus limonensis</i> Olsson, 1922
<i>Antillophos limonensis</i> (Olsson, 1922)	<i>Compsodrillia moenensis</i> (Gabb, 1881)
<i>Cantharus tortuguera</i> Olsson, 1922	<i>Cerodrillia limonetta</i> (Olsson, 1922)
<i>Metula limonensis</i> Olsson, 1922	<i>Knefastia limonensis</i> (Olsson, 1922)
<i>Nassarius caribbeus</i> (Gabb, 1881)	plus 40 undescribed taxa

was deposited, the Caribbean Basin had been subjected to the effects of several glacial episodes, and the composition of the Moín fauna already indicating a significant loss of Mio-Pliocene species, with many groups now considered to be Paciphilic and a number of extinct species characteristic of somewhat older formations, especially the Bowden Formation of Jamaica. It should be noted that although the Bowden is not very much older (considered here as early Late Pliocene) and is geographically close, a substantial portion of its fauna had disappeared by Moín time. Clearly, the differences between the faunas of the Bowden and Moín Formations highlight the effects of one or more of the earlier glacial pulses of the Late Pliocene.

A small but notable constituent of the Moín fauna is defined by those species extending their geographic ranges or migrating southwards due to climatic deterioration during the Tertiary. Among these are *Trivia* cf. *T. crovae* (Olsson, 1967), *Jenneria* cf. *J. richardsi* Olsson, 1967, and *Niso willcoxiana* Dall, 1889. These species, or

Table 2. Mio-Pliocene species whose last occurrence is in the Moín Formation.

<i>Calliostoma guppyana</i> Gabb, 1881	<i>Conus gracillissimus</i> Guppy, 1866
<i>Turbo saltus</i> Olsson, 1922	<i>Conus recognitus</i> Guppy, 1867
<i>Arene lepidota</i> Woodring, 1928	<i>Scobinella morieri</i> Laville, 1913
<i>Microstelma cepula</i> (Guppy, 1866)	<i>Polystira barretti</i> (Guppy, 1896)
<i>Modulus basileus</i> Guppy, 1878	<i>Miraclathurella vittata</i> Woodring, 1928
<i>Atlanta diamesa</i> Woodring, 1928	<i>Glyphostoma moinica</i> Olsson, 1922
<i>Niso willcoxiana</i> Dall, 1889	<i>Nannodiella amicta</i> (Guppy, 1896)
<i>Cancilla limonensis</i> (Olsson, 1922)	<i>Saccharoturrus consentanea</i> (Guppy, 1986)
<i>Conus wiedenmayeri</i> Jung, 1965	<i>Bactrocythara obtusata</i> (Guppy, 1896) plus 6 undescribed taxa

their immediate ancestors, were characteristic members of the faunas of the Pliocene Pinecrest Formation and were absent from contemporaneous faunas in the Caribbean. Despite their subsequent occurrence in the Moín Formation, they are absent from contemporaneous Late Pliocene and Pleistocene formations in Florida, indicating a complete displacement of these species by Plio-Pleistocene glacial episodes to the southern Caribbean. Their appearance in the Moín is also their last before complete extinction, resulting from succeeding glacial pulses.

Of particular interest is the *Conus cedonulli* complex, represented in the Moín by *C. ultimus* Pilsbry and Johnson, 1917. The Mio-Pliocene ancestor of this group was *C. consobrinus* G. B. Sowerby I, 1850, that was distributed throughout the Caribbean basin. The species was subsequently restricted southwards to isolated refugia in the southern Caribbean, where it has speciated into a number of sibling species, each with a very limited distribution (Vink and Cosel, 1985). These species live today in a wide arc from the southern Lesser Antilles, along the coast of northern South America and then north to Honduras, although the complex is not as widely distributed as its parent species. Similarly, *C. venezuelanus* Petuch, 1987, a descendent of the widely-distributed Mio-Pliocene *C. planiliratus* G. B. Sowerby I, 1850, survives in a small area in the Golfo de Triste, off northern Venezuela. *C. venezuelanus* evidently had a greater range during Moín time, as it is quite common in the Costa Rica beds.

West African/Mediterranean Influences

Of interest in the Moín Formation also are those faunal elements that are identified with provinces outside of the typical Caribbean. The occurrence of some West African and Mediterranean elements is not entirely unexpected. Ranellids have been shown to have the ability to cross the Atlantic (Scheltema, 1971; Laursen, 1981) and the closely-related bursids appear also to have achieved some level of teleplanic efficiency. *Bufonaria marginata* (Gmelin, 1791) is restricted to the eastern Atlantic and Mediterranean today and throughout its fossil history, except for the occurrence of four individuals (so far) in the Moín Formation. Teleplanic efficiency may be increased by glacially-induced lowered sea temperatures, as suggested by Beu (1970), by delaying larval metamorphosis just long enough to enable an occasional individual to survive the trans-Atlantic crossing. These particular individuals were able to develop into adults here in the southwestern Caribbean, but apparently were never numerous enough to establish a permanent population. Beu (pers. comm.) identified several individuals of *Bursa scrobilator* (Linné, 1758) from the Moín as well. This West African taxon does have a somewhat longer history in the western Atlantic, having been described as *B.*

mexicana Perrilliat, 1963, from the Agueguexquite Formation. *B. scrobilator* is now restricted to the eastern Atlantic. Other ampho-Atlantic species occurring in the Moín include *Cerithium guinaicum* Philippi, 1849, *Phalium granulatum* (Born, 1778), *Polinices lacteus* (Guilding, 1843), *Pterotyphis pinnatus* (Broderip, 1833), and *Typhis sowerbii* Broderip, 1833, although there is not enough evidence to determine unequivocally whether these taxa originated in the western or eastern Atlantic.

Connections with the Indo-Pacific

The deep-water barrier between the Indo-West Pacific and the eastern Pacific has only been breached since Late Pliocene (Vermeij, 1978), or perhaps even later, with the migration of some elements of reef-associated faunas. The occasional incursion of teleplanic Indo-Pacific species today into the Panamic province is well-documented (Emerson, 1967 and 1978; Houbrick, 1968; Montoya, 1983), although the establishment of permanent populations of such species is for the most part restricted to offshore island groups, including Cocos, Clipperton and the Galápagos Islands (Hertlein, 1937, 1963; Hertlein and Emerson, 1953; Emerson, 1991). Unfortunately, it is not clear whether species of Indo-Pacific origin crossed into the Caribbean prior to the closure of the last trans-Isthmian seaways. Vermeij (1978) suggested that a warming of the waters around southern Africa during the Pliocene permitted the invasion of marine angiosperm grasses from the Indo-West Pacific. The occurrence of *Smaragdia viridis* (Linné, 1758), *Turbo pittieri* (Dall, 1912) (a turbinid closely related to *T. petholatus* Linné, 1758), *Charonia tritonis variegata* (Lamarck, 1816), *Bursa rhodostoma thomae* (d'Orbigny, 1842) and *Gyrineum louisae* Lewis, 1974 (Robinson, 1990), in the Late Pliocene and early Pleistocene Caribbean Basin supports this possible invasion route; belonging to typically Indo-Pacific supra-specific taxa, they are absent from the eastern Pacific (Panamic) waters and there is no fossil record of their ever having been established in that region.

The first "modern" Caribbean fauna

The Moín fauna represents the first fossil Caribbean fauna that is essentially modern in aspect. Two hundred and seventeen prosobranch gastropod species identified (approximately 71% of the total) are still extant and for the most part, their Moín occurrence represents their first in the fossil record. The environments represented by these species range from the intertidal zones (including mangrove, rock and sand environments), through the various reef zones (lagoonal, back-reef, reef crest and fore-reef environments), with deposition occurring at the base of the fore-reef system at depths of 100 to 200 m. The systematic composition

of the fauna has also provided interesting insights into the zoogeography of the region.

It should be made clear that the majority of the living species represented in the Moín fauna are pan-Caribbean in distribution. Smaller numbers of species have a more restricted distribution in the western and/or southern Caribbean, but excessive focus on these particular taxa without keeping in perspective the overall Caribbean nature of the fauna could lead to premature conclusions regarding the subdivision of the Caribbean Province as a whole. The general area is poorly known and for many species, their geographic range is not yet defined. Those Moín species that are living today (or that have a recognizable direct living descendent) and appear to be characteristic of an area extending from the Gulf of Honduras south to Panamá and the adjacent northern Colombian coastline, are listed in Table 3.

Another group of species (Table 4), appear to have a southern Caribbean bias, extending from Costa Rica south to Panamá and east along the northern coast of South America, with some ranging farther south to Surinam and Brazil. It should be noted, however, that some taxa occurring as fossils in Costa Rica, have yet to be found along that coast and are currently known from Colombia or Venezuela and farther east and south, e.g. *Siratus springeri* (Bullis, 1964). Three Moín species that have a southern distribution but occur in two disjunct populations in the southwestern and southeastern Caribbean (not having been reported from the central area), are *Cyclostremiscus schrammi* (P. Fischer, 1857), *Metula lintea* Guppy, 1882 and *Siponochelus tityrus* F. Bayer, 1971.

CONCLUSIONS

The gradual accumulation of both paleontological and neontological systematic and zoogeographic data, of which the current study represents only a fragment, is slowly adding to our understanding of Caribbean zoogeography. The emerging picture is one that is far more complex than

Table 4. Moín species with a southern Caribbean distribution.

<i>Astraliium brevispinum</i> (Lamarck, 1822)	<i>Scaphella evelina</i> F. Bayer, 1971 (represented in the Moín by an undescribed but related species)
<i>Sconsia lindae</i> Petuch, 1987	<i>Conus baylei</i> Jousseaume, 1872
<i>Siratus springeri</i> (Bullis, 1964)	<i>Conus venezuelensis</i> Petuch, 1987
<i>Murexsul harasewychi</i> Petuch, 1987	<i>Hindsiclava</i> cf. <i>H. chazellei</i> (Dautzenberg, 1900)
<i>Fusinus caboblanquensis</i> Weisbord, 1962	<i>Persicula interruptolineata</i> (Megerle von Mühlfeld, 1816)

that of adjacent provinces. Although the Panamic and Carolinian provinces seem to be relatively homogeneous, with a large proportion of the molluscan species occurring throughout the extent of their respective provinces, the Caribbean appears to be fragmented, with numerous species having quite restricted geographic ranges. The nature of this subdivision, however, remains poorly understood. The implications of this study indicate the possibility of the existence of a western Caribbean and a southern Caribbean fauna. It should be stressed again, however, that the evidence so far does not yet justify the designation of zoogeographic entities on the Subprovince level, particularly in view of the limited numbers of species involved. Just as there are species that apparently define a faunule, there are others whose distribution extend outside the implied boundaries of such a faunule and may even span two such entities, or may change through time. Earlier attempts to subdivide the western Caribbean into subprovinces or faunules (Petuch, 1981, 1990) have been based on small numbers of species. The taxonomic status of a number of newly described taxa used to define these faunas has yet to be fully evaluated and their relationship with closely related taxa is not clearly understood. The Moín taxa and their living descendants do not fit into these subprovincial units and they therefore cannot be used to support these hypothetical constructs. A great deal more work needs to be done in terms of systematics and biogeography of the species (non-molluscan, as well as molluscan) assumed to be endemic to the area before subprovincial boundaries can be defined.

Table 3. Moín species that have a western Caribbean distribution.

<i>Stephopoma myrakeenae</i> Olsson and McGinty, 1958	<i>Voluta virescens</i> Lightfoot, 1786 (including the various named forms)
<i>Cerithioclava garciai</i> Houbrick, 1985	<i>Agaronia mancinella</i> (Olsson, 1922) (represented by today by <i>Agaronia hilli</i> Petuch, 1987 and <i>A. leonardhilli</i> Petuch, 1987)
<i>Cerithiopsis caribbaeus</i> (Gabb, 1881)	<i>Conus spurius quadratus</i> Röding, 1798
<i>Haustellum olssoni</i> (E. Vokes, 1967)	<i>Fusinus gabbi</i> Grabau, 1904
<i>Muricopsis deformis</i> (Reeve, 1846)	
<i>Siponochelus bullisi</i> Gertman, 1969	
<i>Olivella myrmecoon</i> Dall, 1912	
<i>Hindsiclava tippetii</i> Petuch, 1987	

ACKNOWLEDGMENTS

The author gratefully acknowledges the help of many individuals who helped in numerous ways during the course of this project. In particular, Emily H. Vokes of Tulane University, New Orleans, without whose help and support it would never have been completed. For their help in the field, J. Michel Montoya of San José, Costa Rica; Goldie Cooper, Ronald Ebanks, and Richard McNab of Roatán of the Bay Islands, Honduras; James Ernest of Panamá City, Panamá; Matthew C. Redmond V of Golden, Colorado; and Richard J. Kirshner of New Orleans, Louisiana.

For their input and discussion, I would like to thank Gary Rosenberg and Elana Benamy of the Academy of Natural Sciences of Philadelphia. I am also grateful for the helpful comments and suggestions of two anonymous reviewers of an earlier draft of this paper.

LITERATURE CITED

- Akers, W. H. 1972. Planktonic foraminifera and biostratigraphy of some Neogene formations, northern Florida and the Atlantic coastal plain. *Tulane Studies in Geology and Paleontology* 9:1-139.
- Beu, A. G. 1970. The mollusca of the genus *Charonia* (Family: Cymatiidae). *Transactions of the Royal Society of New Zealand, Biological Sciences* 11:205-233.
- Cassell, D. T. 1986. *Neogene foraminifera of the Limón Basin of Costa Rica*. Doctoral dissertation, Louisiana State University, Baton Rouge, Louisiana. 323 pp.
- Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Byell, P. Jung and J. A. Obando. 1992. Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and western Panama. *Geological Society of America Bulletin* 104:814-828.
- Emerson, K. 1967. Indo-Pacific faunal elements in the tropical eastern Pacific, with special reference to the mollusks. *Venus* 25(3-4): 85-93.
- Emerson, K. 1978. Mollusks with Indo-Pacific affinities in the eastern Pacific Ocean. *Nautilus* 92:91-96.
- Emerson, K. 1991. First records for *Cymatium mundum* (Gould) in the eastern Pacific Ocean, with comments on the zoogeography of the tropical trans-Pacific Tonnacean and non-Tonnacean prosobranch gastropods with Indo-Pacific faunal affinities in western American waters. *Nautilus* 105:62-50.
- Gabb, W. M. 1881. Description of new species of fossils from the Pliocene Clay Beds between Limón and Moen, Costa Rica, together with notes on previously known species from there and elsewhere in the Caribbean area. *Journal of the Academy of Natural Sciences of Philadelphia* (Series 2) 8:349-380.
- Gertman, R. L. 1969. Cenozoic Typhinae (Mollusca: Gastropoda) of the western Atlantic region. *Tulane Studies in Geology and Paleontology* 7:143-191.
- Hertlein, L. G. 1937. A note on some species of marine mollusks occurring in both Polynesia and the western Americas. *Proceedings of the American Philosophical Society* 78:303-312.
- Hertlein, L. G. 1963. Contribution to the biogeography of Cocos Island, including a bibliography. *Proceedings of the California Academy of Sciences* (Series 4) 32:219-289.
- Hertlein, L. G. and W. K. Emerson. 1953. Mollusks from Clipperton Island (eastern Pacific) with the description of a new species of gastropod. *Transactions of the San Diego Society of Natural History* 11:345-364.
- Houbrick, R. S. 1968. New record of *Conus ebraeus* in Costa Rica. *Veliger* 1:292.
- Knight, J. B., L. R. Cox, A. M. Keen, A. G. Smith, R. L. Batten, E. L. Yochelson, N. H. Ludbrook, R. Robertson, C. M. Yonge and R. C. Moore. 1960. *Treatise on Invertebrate Paleontology* (ed. R. C. Moore). Part 1. *Mollusca*, 351 pp.
- Laursen, D. 1981. Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. *Dana Report* No. 89, 43 pp.
- Montoya, J. M. 1983. Los moluscos marinos de la Isla del Coco, Costa Rica. 1. Lista anotada de especies. *Brenesia* 21:325-353.
- Olsson, A. A. 1922. The Miocene of northern Costa Rica, with notes on its general stratigraphic relations. *Bulletins of American Paleontology* 9:179-460.
- Petuch, E. J. 1981. A volutid species radiation from northern Honduras, with notes on the Honduras Caloosahatchian secondary relict pocket. *Proceedings of the Biological Society of Washington* 94:1110-1130.
- Petuch, E. J. 1990. A new molluscan faunule from the Caribbean coast of Panama. *Nautilus* 104(2):57-71.
- Robinson, D. G. 1990. On the occurrence of *Gyrineum* in the early Pleistocene Moín Formation of Costa Rica. *Tulane Studies in Geology and Paleontology* 23:133-135.
- Robinson, D. G. 1991. *The systematics and paleoecology of the prosobranch gastropods of the Pleistocene Moín Formation of Costa Rica*. Doctoral dissertation, Tulane University, New Orleans, Louisiana. 749 pp.
- Robinson, D. G. and J. M. Montoya. 1988. Los moluscos marinos de la costa Atlántica de Costa Rica. *Revista de Biología Tropical* 35:375-400.
- Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* 140:284-322.
- Taylor, G. D. 1975. *The Geology of the Limon area of Costa Rica*. Doctoral dissertation, Louisiana State University, Baton Rouge, Louisiana. 116 pp.
- Vermeij, G. J. 1978. *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press, Cambridge, Massachusetts. 332 pp.
- Vink, D. L. N. and R. von Cosel. 1985. The *Conus cedonulli* complex: historical review, taxonomy and biological observations. *Revue suisse de Zoologie* 92:525-603.
- Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part 2, Gastropods and discussion of results. *Carnegie Institute of Washington, Publication* 385, 564 pp.
- Woodring, W. P. 1957-1973. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks. *United States Geological Survey, Professional Paper* 306 A-E. 539 pp., 82 pl.

Date of manuscript acceptance: 28 April 1993